PROC. BIOL. SOC. WASH.
92(2), 1979, pp. 307–327

STUDIES ON DECAPOD CRUSTACEA FROM THE INDIAN RIVER REGION OF FLORIDA XIII. LARVAL DEVELOPMENT UNDER LABORATORY CONDITIONS OF THE SPIDER CRAB *MITHRAX FORCEPS* (A. MILNE EDWARDS, 1875) (BRACHYURA: MAJIDAE)

Kim A. Wilson, Liberta E. Scotto, and Robert H. Gore

Abstract.—The complete larval development of *Mithrax* (*Mithraculus*) *forceps,* a common shallow water marine spider crab is described and illustrated from stages cultured in the laboratory. Development consists of one prezoeal, two zoeal, and one megalopal stage. Temperature affects the duration of development, with attainment of crab stage I requiring at least 14 days at warm room temperature of 25°C, and 16 days at cool room temperature of 20°C. Morphological features in the larval stages of *M. forceps* were compared with those seen in larvae of two other members of the genus, in an attempt to provisionally distinguish between the larvae of the subgenera *Mithraculus* and *Mithrax*. Larvae of *M. forceps* are nearly identical to those of *Mithrax* (*Mithrax*) *pleuracanthus* but differ substantially from those of *Mithrax* (*Mithrax*) *spinosissimus,* indicating that the subgeneric diagnoses, originally established using adult characters, may need to be reconsidered in the light of larval features. This report is only the second for any species in the genus *Mithrax,* and the first in the subgenus *Mithraculus* for which the complete larval development has been described and illustrated.

The majid crab genus *Mithrax,* presently comprising about 30 species, is a relatively large group of spider crabs restricted to the New World (Rathbun, 1925). The genus is divided into two subgenera, (*Mithrax*) and (*Mithraculus*). *Mithrax* (*Mithraculus*) *forceps,* widely distributed from Bermuda, Cape Hatteras, North Carolina, Gulf of Mexico, Caribbean Sea to Rio de Janiero, Brazil (Williams, 1965) is among the more common of the 10 species in the genus presently known to occur in intertidal marine and nearshore continental shelf waters of the Indian River region on the central eastern Florida coast. However, the larval development in this genus is known,

either completely or in part, for only four species, three of which have been described in publications. These include *M.* (*Mithraculus*) *forceps* (Lebour, 1944; brief description of first zoeal stage), *M.* (*Mithrax*) *pleuracanthus* (Yang, 1967, unpublished; complete description of first zoeal stage), and *M.* (*Mithrax*) *spinosissimus* (Provenzano and Brownell, 1977; complete description of development). Yang (1967, unpublished) also cultured *M.* (*Mithraculus*) *sculptus* and *M. forceps* but provided neither description nor illustrations. There are, thus, few data available for comparative purposes among the larvae of either subgenera.

In this paper we report on the complete larval development of *M.* (*Mithraculus*) *forceps,* cultured in the laboratory, and compare mithraculine larval features, as far as possible, with those exhibited by mithraxine larvae. Our description and illustrations are but the second to be made for the complete larval development of any species in this large, heterogeneous, and widespread genus.

Materials and Methods

Three ovigerous females were collected from the Atlantic Ocean, off Pepper State Park, St. Lucie County, Florida, in 6 m of water, on 28 September 1977, using SCUBA. They were held in 8.5 cm covered glass laboratory dishes in non-flowing seawater of 36‰ until hatching occurred 30 September, 2 October and 4 October, respectively. A total of 384 larvae divided evenly among 16 24-compartmented plastic trays, were cultured in four series as follows: 120 larvae in five trays (1 starved) at cool room temperature (20°C), the same at warm room temperature (25°C), 96 larvae in four trays (1 starved) in a controlled temperature unit (CTU) undergoing diel variation of 25°C (day) and 20°C (night) (12–12 hours), and 48 larvae in two trays at 30°C in a second 12L–12D CTU. Larvae were cultured in the same manner as in previous developmental studies (see e.g. Gore, 1973), and with the exception of the diel variation and 30°C series in the CTU's, were exposed to ambient light, and to warm or cool room temperatures maintained in restricted-access laboratories by reverse-cycle air-conditioning units (daily variation approximately 0.5°C). Water in all culture trays was changed daily, and *Artemia* nauplii were provided as food on a daily basis in all series except the starved trays. Salinity of the stored, culture seawater used throughout the study remained at 36‰. Illustrations and measurements of zoeae and megalopae were made as in previous studies, using a camera lucida, and a slide micrometer in conjunction with an ocular reticle, on either a dissecting stereo- or binocular compound-microscope. Measurements follow the methodology of Provenzano and Brownell (1977) and are expressed as the arithmetic average of the specimens examined in each

Table 1. Duration of the larval stages of *Mithrax forceps* at various temperatures.

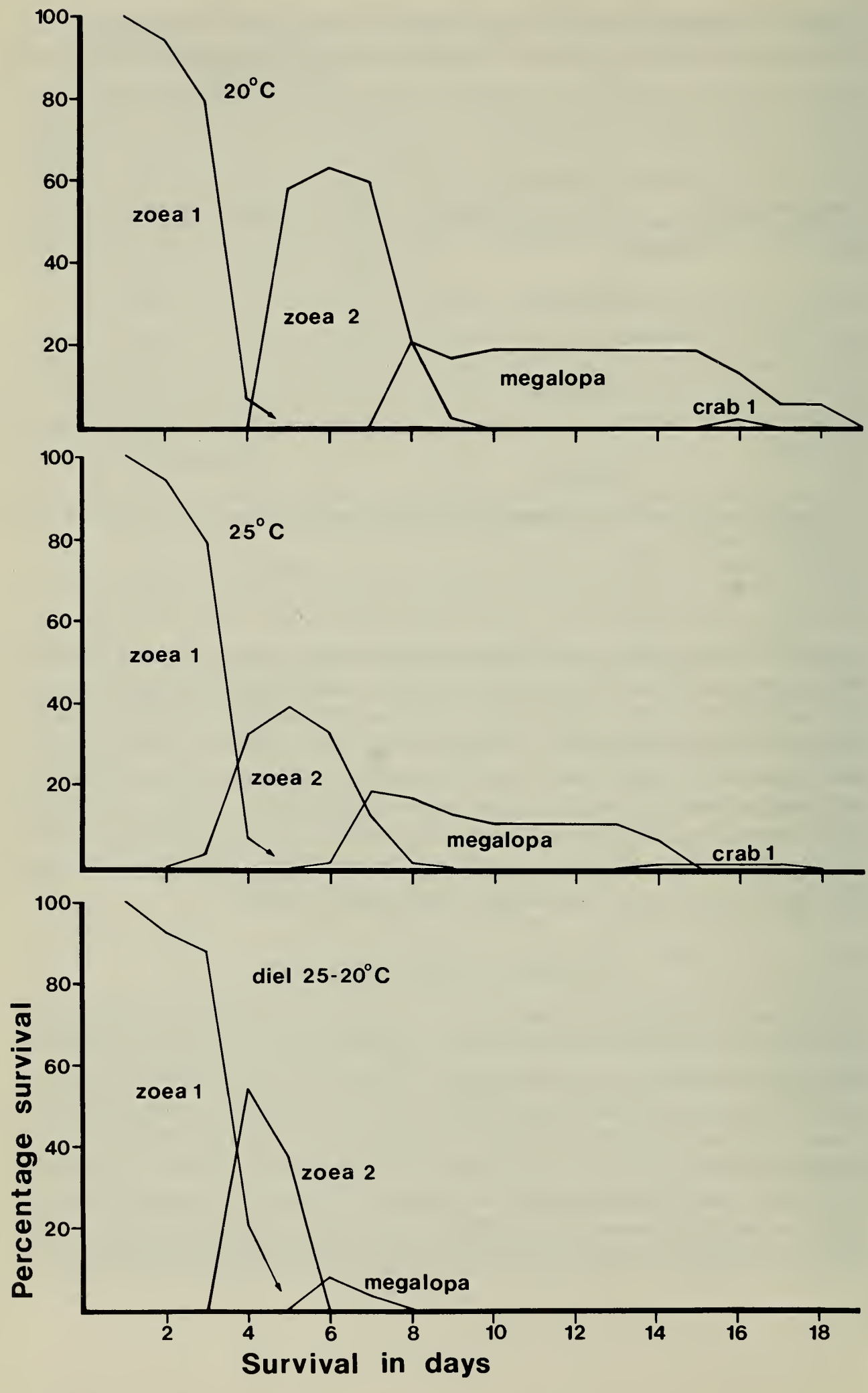
Temperature (°C)		Duration (days) Minimum	Mean	Mode	Maximum	Total number molting to next stage
20°	Zoeae I	4	4.3	4	6	36
	II	2	3.2	3	5	12
	Megalopa	8*	–	–	–	1
25°	Zoeae I	2	3.1	3	4	29
	II	2	3.1	3	4	18
	Megalopa	7*	–	–	–	1
Diel 25°–20°	Zoeae I	3	3	3	3	13
	II	2	2	2	2	2
	Megalopa	2†	–	–	–	0

* Based on single surviving megalopa at each temperature; all other specimens died in stage.
† Died in stage.

stage. The descriptions and illustrations that follow were prepared from the larvae–postlarvae in six trays in which the megalopal stage was attained, viz. two of five trays at 20°C, three of five at 25°C, and one of four undergoing diel variation of 25–20°C. Complete series of larvae and postlarvae, and the females that yielded them, have been deposited in the National Museum of Natural History, Smithsonian Institution (USNM 17158), The British Museum (Natural History) (1979:3, 4), the Allan Hancock Foundation, University of Southern California (1397-01), and (larval–postlarval series only) the Rijksmuseum van Nautuurlijke Historie (D. 31964).

Laboratory Culture Experiment

As in other majid crabs, *Mithrax forceps* passes through a prezoeal, two zoeal, and one megalopal stage before attaining first crab stage. We believe the prezoeal stage to be an integral part of larval development in *M. forceps*, as did Provenzano and Brownell (1977) who also noted a prezoeal stage in *M. spinosissimus*. However, only four prezoeae were observed in a single ancillary hatch of *M. forceps*. A careful examination of hatches used for the following description produced no prezoeae. However, because these three females hatched larvae before 0800 hours in the morning, the possibility cannot be dismissed that a prezoeal stage of brief duration might have oc-


100
80
60
40
20
20°C
zoea 1
zoea 2
megalopa
crab 1
25°C
zoea 1
zoea 2
megalopa
crab 1
diel 25-20°C
zoea 1
zoea 2
megalopa
Percentage survival
2
4
6
8
10
12
14
16
18
Survival in days

curred and had already molted to zoeal stage I by the time the larvae were examined. The prezoeal molt is especially diaphanous and could easily have been overlooked amid the debris of egg casts on the bottom of the covered glass hatching bowl.

The duration of each development stage is presented in Table 1, and the percentage of larval survival is illustrated in Fig. 1. Although some variation in developmental time was seen among the fed series at different temperatures, in general it required at least 14 days (at 25°C), and 16 days (at 20°C) to attain crab stage I. Larvae usually remained in stage I from 3–4 days at all temperatures although some zoeae held at 20°C often required 5 days to reach stage II. Second stage zoeae usually remained as such for 3–4 days at 25°C and 3–5 days at 20°C, so little temporal variation occurred within this instar. Based on rather limited data of two surviving instars the duration of the megalopal stage was also consistent, lasting 8–9 days at both of these temperatures. The duration of development of larvae in the diel-programmed CTU at 25°C paralleled that seen at warm room temperature, but with a slightly shorter second zoeal stage (2 days). No conclusions can be drawn regarding the postlarvae duration because both surviving megalopae died after one and two days in stage, respectively. Larvae in the 30°C CTU did not survive through the second zoeal stage, and all starved zoeae died in stage I.

These results suggest that *M. forceps* can complete its planktonic existence in a period approximating two weeks. This is at variance with the developmental time noted by Provenzano and Brownell (1977) for *M. spinosissimus* which required the relatively short duration of 130–148 hours (5–6 days) to attain first crab stage at temperatures of 24–28°C. Whether this rapid development is more a result of the variable, higher temperatures in their program, or is inherent in the larvae of their species, or perhaps both, cannot be ascertained at present. For our part, we did note a more rapid development in stage II zoeae held in the diel fluctuating temperatures of 25°–20°C so that the megalopal stage was reached after a total zoeal duration of about 5 days (120+ hours). Comparatively, megalopa was reached in *M. spinosissimus* in only 2–3 days (60–70 hours), but because none of our megalopae in the diel program survived, further speculations are unwarranted. However, the results of our differential culturing-temperature program show, as seen in other laboratory-culture studies on decapod larvae, that temperature affects duration of development, with cooler temperatures (i.e. 20°C) increasing developmental time, and warmer temperatures (i.e. 25°C) decreasing it (see Fig. 1).

←

Fig. 1. *Mithrax forceps*: Percentage and duration of survival of larvae cultured under laboratory conditions. See text for explanation of diel variation.

Description of Developmental Stages

First Zoea.—(Carapace length.—70 mm; number of specimens examined, 10).

Carapace (Fig. 2A, a): Cephalothorax smooth, inflated, globose; with short recurved dorsal and straight rostral spine. A dorsal tubercle medially, midway between the bases of dorsal and rostral spines, followed by a pair of minute setae postero-laterally, and a second pair dorso-laterally on cardiac region. Six setae on posterolateral border, first (=anterior seta, Yang 1967) by far the strongest (Fig. 2a). Thoracic appendages unsegmented, extending slightly below posterolateral margin of carapace. Eyes unstalked.

Abdomen (Fig. 2A): Five somites, all with pair of small setae posterodorsally; second with pair of small lateral spines curving anteriorly; third through fifth each with a single short spine on posteroventral angle. Pleopod primordia on second through fifth somites amorphous, subdivided.

Telson (Fig. 2B): Trapezoidal, not deeply excavated posteriorly, but with elongate furcae; latter covered with small fine hairs and carrying a pair of lateral movable spines at base; posterior margin of telson with 6 stout setae, armed with rows of spinules.

Antennule (Fig. 2C): A conical rod; 2 long stout, and 2 thinner, short terminal aesthetascs, plus 1 fine hair.

Antenna (Fig. 2D): Protopodite a slender dagger-like process bearing 2 rows of small teeth from midlength distally to tip. Exopodite tapered, equal to or slightly longer than protopodite; distal quarter with 2 rows of small teeth; a slender serrated spine and a naked seta distally. Endopodite bud naked, ⅓ length of protopodite.

Mandible (Fig. 2E): Asymmetrically dentate, scoop-shaped processes. Left incisor margin with 5 distinctly rounded prominences; molar irregularly dentate; 3 rounded prominences at junction of molar and incisor of left side (ventral view); right side with 1 prominence.

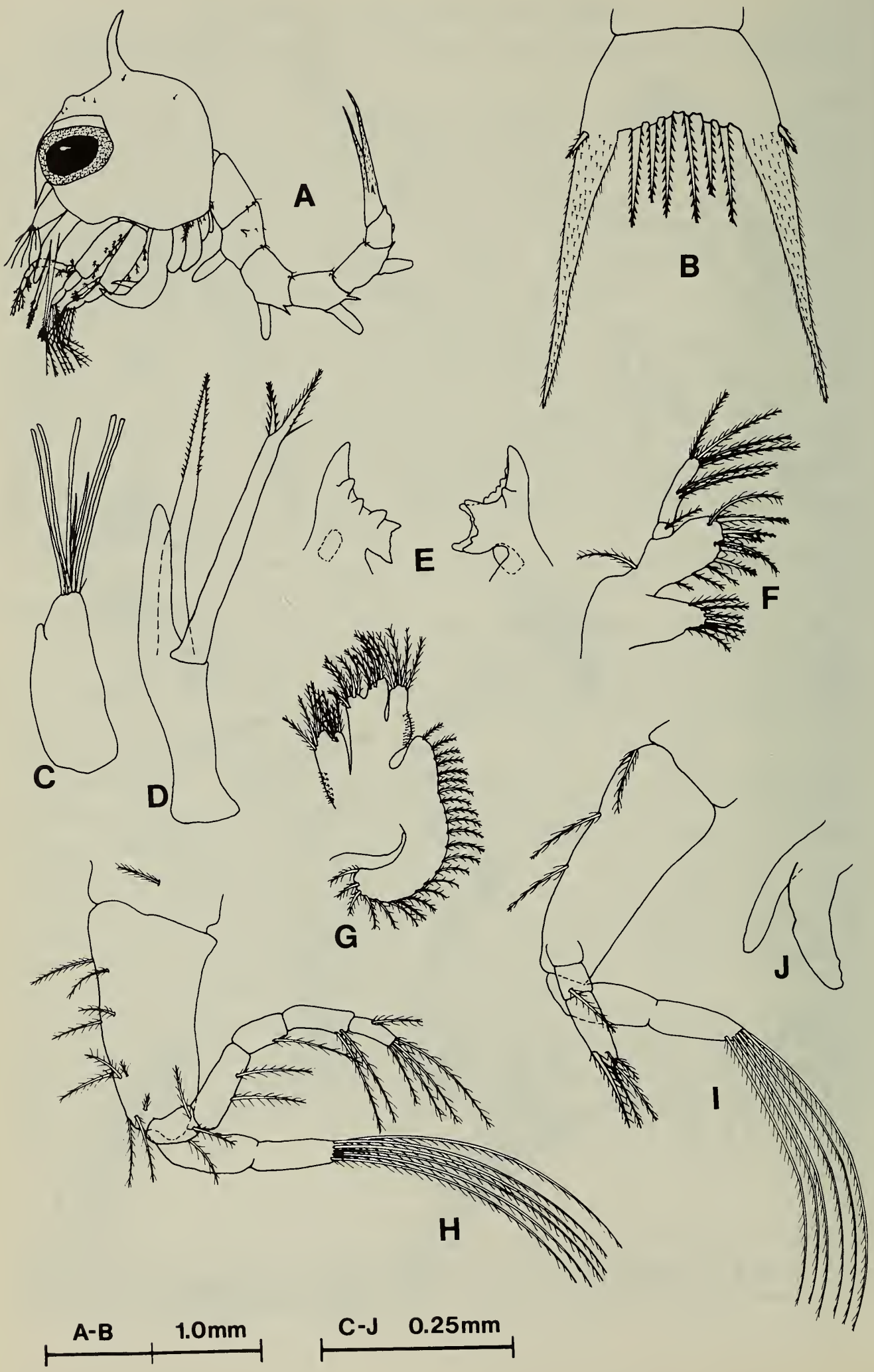
Maxillule (Fig. 2F): Endopodite 2-segmented; proximal short, with 1 long feathery seta laterally, distal longer, with 4 unequal terminal setae plus 2 longer setae subterminally. Coxal and basal endite each with 7 terminal processes, 5 of which on basal endite are stouter.

Maxilla (Fig. 2G): Endopodite unsegmented, 5 terminal setae. Proximal and distal lobes of coxal and basal endites each with 5, 4 setae, respectively; pubescence on basal endite and endopodite as illustrated. Scaphognathite with 13 plumose setae on outer margin, distal setae increasing in stoutness, as in detail (Fig. 2g).

→

Fig. 2. *Mithrax forceps*, first zoea: **A**, Lateral view; **a**, Detail of posterolateral margin of carapace; **B**, Telson; **C**, Antennule; **D**, Antenna; **E**, Mandibles; **F**, Maxillule; **G**, Maxilla; **g**, Detail of scaphognathite apex; **H**, Maxilliped 1; **I**, Maxilliped 2.


a
A
a
B
C
D
E
F
G
g
H
I
A-B 1.0 mm
a,C-I 0.25mm


A
B
C
D
E
F
G
H
I
J
A-B 1.0mm
C-J 0.25mm

Maxilliped 1 (Fig. 2H): Coxopodite with 1 seta. Basipodite with 10 setae, progressing distally, 2, 2, 3, 3. Endopodite 5-segmented, ventral setal formula progressing distally 3, 2, 1, 2, 4 + I (roman numeral denotes dorsal seta). Exopodite incompletely 2-segmented, 4 terminal natatory setae.

Maxilliped 2 (Fig. 2I): Coxopodite naked. Basipodite with 3 ventral setae. Endopodite 3-segmented, ventral setal formula progressing distally 0, 1, 5; heaviest seta placed laterally. Exopodite as in maxilliped 1.

Color: Zoea transparent overall; frontal region, gut region and dorsal surface of abdominal somites pale gold; abdominal somites 2, 3, 4, orange ventrally, fifth only faintly so. Several spider-like black chromatophores on labrum and mandible; a line of same extends interiorly from gut through second abdominal somite, spreading only slightly into third. Gut green interiorly. Eyes turquoise in reflected light, corneas dark.

Second Zoea.—(Carapace length.—0.82 mm; number of specimens examined, 10).

Carapace (Fig. 3A): Cephalothorax essentially unchanged in general form from stage I, but larger, more inflated, dorsal spine proportionately shorter. Paired dorsal setae now include 2 interocular, 2 posterolateral to dorsal tubercle, 1 at each lateral base of dorsal spine, plus pair previously noted dorsolaterally on cardiac region. Carapacial setation on posterolateral margin now 1 strong, 6 finer. Thoracic appendages longer but remain unsegmented. Eyes stalked, a minute ocular tubercle on anterior margin.

Abdomen (Fig. 3A): Six somites; first with 3 setae on posterodorsal margin, second with one median and one posterodorsal pair, third through fifth unchanged from stage I. Lateral spine on somite 2 unchanged, spines posteroventrally on somites 3–5 more elongate than in stage I; sixth somite now with single spine on posteroventral angle. Pleopod buds well-developed on somites 2–5, rudimentary on somite 6.

Telson (Fig. 3B): Similar in form and marginal setation to first stage. Furcae same length as stage I but now 3 times length of reduced telson, maintaining posterior spines and hairs.

Antennule (Fig. 3C): Endopodite bud present, placed as shown. Seven unequal aesthetascs and single fine hair terminally.

Antenna (Fig. 3D): Similar in form and armature to first stage. Endopodal bud lengthened, now nearly ½ protopodite process.

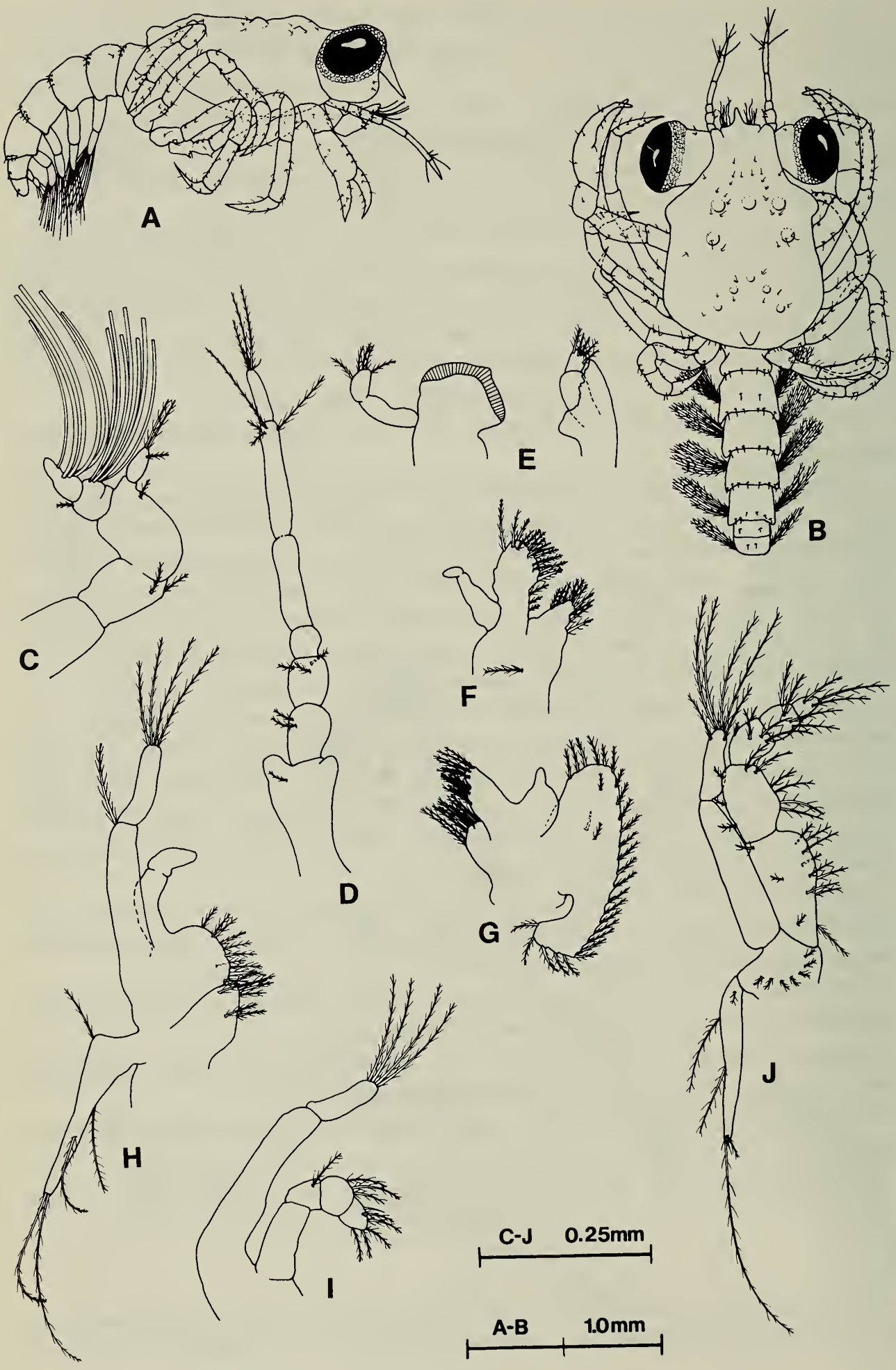
Mandible (Fig. 3E): As in first stage; palp bud present on each anterior surface.

Maxillule (Fig. 3F): Endopodite unchanged. Coxal endite with 7, basal

---

←

Fig. 3. *Mithrax forceps*, second zoea: **A**, Lateral view; **B**, Telson; **C**, Antennule; **D**, Antenna; **E**, Mandibles; **F**, Maxillule; **G**, Maxilla; **H**, Maxilliped 1; **I**, Maxilliped 2; **J**, Maxilliped 3.


A
B
C
D
E
F
G
H
I
J
C-J 0.25mm
A-B 1.0mm

endite with 10, processes of varying stoutness; a single seta dorsally on lower outer margin of basal endite.

Maxilla (Fig. 3G): Endopodite and coxal endites unchanged in form and setation from first stage, basal endite now with 5 setae on each lobe. Scaphognathite with 24 plumose marginal setae.

Maxilliped 1 and 2 (Figs. 3H, I): Similar to first stage; exopodite on each with 6 terminal natatory setae.

Maxilliped 3 (Fig. 3J): Naked, bilobed, rudimentary process.

Color: Cephalothorax and abdominal coloration similar to first stage. Position and color of chromatophores essentially unchanged except for additional black chromatophore on carapace posterio-dorsad to each eye; chromatophores on gut and maxilliped 2 more pronounced, that on maxilliped 1 now lacking. Eye color similar to stage I.

Megalopa.—(Carapace length × width.—1.06 × 0.96 mm; number of specimens examined; 10).

Carapace (Fig. 4A, B): Cephalothorax generally ovally subquadrate, with well developed supraocular lobes, outer orbital angles bluntly produced; frontal region rectangular, rostrum elongate, deflexed, spiniform. Gastric region with 3 large transverse tubercles, plus a pair immediately behind outer 2; cardiac region with 5 small tubercles forming an arch. Single, largest tubercle on intestinal region. Eyes large, anterior margin of eyestalks with 2 small setae.

Abdomen (Fig. 4A–B, 5A–C): Abdominal pleura 2–5 with lobes at posteroventral angles, that of sixth subquadrate, all with minor setation placed as shown. Telson smooth, subquadrate, posterior angles rounded, 2 dorsomedial setae. Pleopods of decreasing size on somites 2–6, with 11, 11, 11, 9, 5 setae on each exopodite, respectively. Endopodites on pleopods 1–4 without setae but with appendix interna; pleopod 5 (=uropod) without endopod or appendix interna.

Antennule (Fig. 4C): Biramous. Peduncle partly or completely 3-segmented; basal segment naked, second with 2, third with 1 distal, setae. Lower ramus with 3 setae, placed 2 terminally, 1 subterminally; upper ramus 2- or incompletely 3-segmented; penultimate with 7 aesthetascs placed in V, progressing distally 2, 2, 2, 1, plus 1 short distoventral seta; terminal segment with 5 aesthetascs, progressing distally as 4, 1.

Antenna (Fig. 4D): Peduncle with 2 distolateral lobes and a single seta. Setation of the 6 flagellar segments proceeding distally 2, 3, 0, 0, 4, 3, plus 1 hair.

←

Fig. 4. *Mithrax forceps*, megalopa, sensory and feeding appendages: **A**, Lateral view; **B**, Dorsal view; **C**, Antennule; **D**, Antenna; **E**, Mandibles; **F**, Maxillule; **G**, Maxilla; **H**, Maxilliped 1; **I**, Maxilliped 2; **J**, Maxilliped 3.

Mandible (Fig. 4E): Incisor now truncately spatulate, margin heavily chitinized. Palp indistinctly 2-segmented, with 0, 5 setae, respectively. Molar process irregularly serrate.

Maxillule (Fig. 4F): Endopodite indistinctly 2-segmented, naked. Coxal endite with 10, basal endite with 18, marginal processes of varying stoutness; latter retains 1 long feathery seta on lower margin.

Maxilla (Fig. 4G): Endopodite inflated, unsegmented, naked. Setation on proximal and distal lobes of coxal and basal endites 7, 3, and 6, 6, respectively. Scaphognathite with 26–30 setae on outer margin, plus 3 laterally on either side of blade.

Maxilliped 1 (Fig. 4H): Endopodite partly 2-segmented, naked. Exopodite 2-segmented, setation 1, 4, respectively. Coxal endite with 5–7, basal endite 9–11, marginal setae. Epipodite with 1 proximal, and up to 5 distal, setae.

Maxilliped 2 (Fig. 4I): Endopodite 4-segmented; setation progressing distally 0, 1, 3, 6. Exopodite 2-segmented, 4 terminal setae. Epipodite absent.

Maxilliped 3 (Fig. 4J): Endopodite 5-segmented, setal formula progressing distally usually 12, 9, 5, 4–6, 3–4. Exopodite 2-segmented, 6 terminal setae. Epipodite usually with 5, rarely 6, setae in illustrated positions. Protopodite ringed with 5–7 short setae.

Pereiopods (Fig. 5D–F): Chelipeds large, elongate, equal, setose. Manus smooth, inner and outer surface with scattered hairs; propodus with several small teeth distally on cutting edge, tip slightly hooked, overlapping dactyl exteriorly when closed; dactyl smooth, curved, setae as shown. Pereiopods 2–5 (walking legs 1–4) similar in form, setation sparse to moderate, as illustrated, all without supernumerary teeth on dactyls; as in other majid megalopae pereiopod 5 lacking "brachyuran feelers."

Color: Carapace overall a pale golden-brown; frontal region pale greenish-gold. Gut interiorly iridescent green, with paired black chromatophores dorsally and posterolaterally. Mandible, labrum and protopodite of third maxilliped with several interlocking black chromatophores dorsally and posterolaterally. Coxopodite of cheliped with one black, one red-orange chromatophore ventrally; coxopodite and carpus of second through fifth pereiopods with a single pale red chromatophore ventrally. A single black chromatophore dorsally on anterior margin of abdominal somite 1; several spider-like red chromatophores at junction of somites 2–3; numerous, interspersed red and black chromatophores similarly placed at junctions of somites 3–4, 4–5, 5–6. Junction of somite 6 and telson pale greenish-gold, overlain with several small spidery black chromato-

---

→

Fig. 5. *Mithrax forceps*, megalopal locomotory appendages: **A–C**, Pleopods 1, 4, 5; **D–F**, Pereiopods 1, 3, 5.

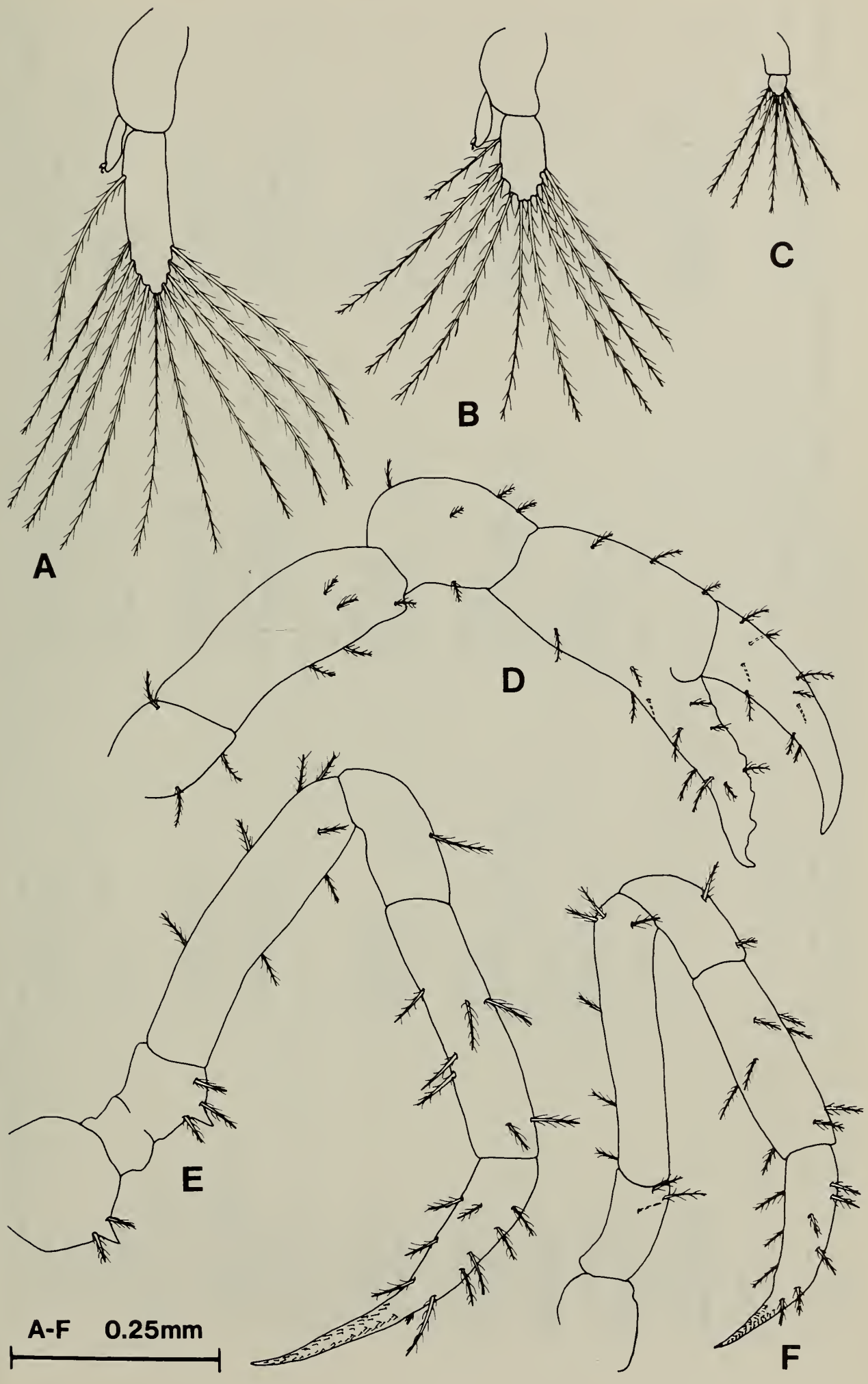

A
B
C
D
E
F
A-F 0.25mm

Table 2. Summary of larval and postlarval characters in known species of *Mithrax*.

	M. forceps	*M. pleuracanthus*	*M. spinosissimus*
ZOEA I			
CARAPACE			
Posterolateral setae	1 + 5	1 + 5	No data
ANTENNULE			
Aesthetascs	4 + hair	3 + hair	5, no hair
ANTENNA			
Endopod: Protopod	Endo. ⅓ proto. length	Endo. ⅓ proto. length	Endo. ½ proto. length
Exopod	Entire, 0 terminal seta	Entire, 0 terminal seta	Strong terminal seta
MANDIBLE	No palp	No palp	No palp
MAXILLULE			
Endopod	2 segs; 1, 2 + 4 setae	2 segs; 1, 2 + 4 setae	1 seg; 2 setae
Basal endite	7 processes	7 processes	6 processes
Coxal	7 processes	7 processes	5 processes, 2 basal setae
MAXILLA			
Endopod	5 terminal setae	5 terminal setae	1 subterminal seta
Basal endite	5, 4 processes	5, 4 processes	3, 3 processes
Coxal endite	5, 4 processes	5, 4 processes	1, 1 process
Scaphognathite	13 marginal setae	13 marginal setae	30 marginal setae
MAXILLIPED 1			
Coxopod	1 seta	No data	No data
Basipod	2, 2, 3, 3 setae	2, 2, 3, 3 setae	No data
Endopod	3, 2, 1, 2, 4 + I setae	3, 2, 1, 2, 4 + I setae	0, 1, 1, 2, 3–4 + I setae
Exopod	4 natatory setae	4 natatory setae	4 natatory setae

Table 2. Continued.

	M. forceps	*M. pleuracanthus*	*M. spinosissimus*
MAXILLIPED 2			
Coxopod	0 setae	No data	No data
Basipod	1, 1, 1 setae	1, 1, 1 setae	No data
Endopod	0, 1, 5 setae	0, 1, 4 setae	Unsegmented; 1 or 1, 1, 1 setae
Exopod	4 natatory setae	4 natatory setae	4 natatory setae
MAXILLIPED 3	Amorphous bud	Amorphous bud	Biramous; faintly segmented
ABDOMEN	5 somites	5 somites	5 somites
	Spines on som. 2–5	Spines on som. 2–5	Spines on som. 2–5
	Pleopod primordia +	Pleopods absent	Pleopod buds +
TELSON	No median notch	Minute median notch	Distinct median notch
	Posterior margin truncate, transverse		Posterior margin deeply excavate

Table 2. Continued.

	M. forceps	*M. spinosissimus*	*M. forceps*	*M. spinosissimus*
ZOEA II			MEGALOPA	
CARAPACE				
Posterolateral setae	1 + 6	No data	5 gastric, 5 cardiac tubercles	5 gastric, 3 cardiac tubercles
ANTENNULE	Endopod bud +	No endopod bud		
Aesthetascs	7 + hair	5, no hair	(2, 2, 2, 2, 1) (4, 1)	(5) (3, 1)
ANTENNA	Endopod unsegmented	Endopod segmented		
Endopod: Protopod	Endopod ½ protopod	Endopod ⅔ protopod		
Exopod	As in stage 1	As in stage 1	1, 2, 3, 0, 0, 4, 3,+1 hair	2, 2, 2, 0, 0, 4, 3, no hair
MANDIBLE	Palp bud +	Palp bud +	5 terminal setae	3 terminal, 2 subterminal
MAXILLULE				
Endopod	As in stage I	As in stage I	2 segments; 0 seta	1 segment; 0 seta
Basal endite	10 processes	7 processes	18 processes	12–15 processes
Coxal endite	7 processes	5 processes	10 processes	8 processes
MAXILLA				
Endopod	5 terminal setae	2 subterminal setae	Blunt tip; 0 seta	Sharp tip; 0 seta
Basal endite	5, 5 processes	2, 2 processes	6, 6 processes	5–6, 5–6 processes
Coxal endite	5, 4 processes	1, 1 processes [2, 2]*	7, 3 processes	"3–5 each"
Scaphognathite	24 marginal setae	31 marginal setae	26–30 marginal, 3 lateral setae	33–37 marginal, 0 lateral setae
MAXILLIPED 1				
Coxopod	1 seta	No data	5–7 setae	"16" [=6 + 10?] setae
Basipod	2, 2, 3, 3, setae	No data [epipod +?]*	9–11 setae	on "protopodite"
Endopod	As in stage I	0, 1, 1, 1, 3–4 [1, 1, 1, 1, 4]*	2 segments; 0 seta	1 segment; 0 setae
Exopod	6 natatory setae	6 natatory setae	1, 4 setae; epipod with 5 setae	0, 4–6 setae; epipod with 4 setae

Table 2. Continued.

	M. forceps	*M. spinosissimus*	*M. forceps*	*M. spinosissimus*
MAXILLIPED 2				
Coxopod	0 seta	No data	Fused with basipodite; no setae noted	
Basipod	1, 1, 1 setae	No data		
Endopod	0, 1, 5 setae	Unsegm; 2 subterm. setae	4 segments; 0, 1, 3, 6 setae	5 segments; 0, 0, 1, 3, 6
Exopod	6 natatory setae	6 natatory setae	0, 4 setae	0, 4–6 setae
MAXILLIPED 3	Rudimentary, bilobed, naked	Biramous, endopod and exopod segmented, naked	Protopod with 5–7 setae Endopod unarmed	Protopod with 4 setae Endopod dentate
			Exopod with 0, 6 setae	Exopod with 0, 4 setae
ABDOMEN	6 somites	6 somites [see text]*		
	As in stage I	As in stage I	Similar in form and setation in both species	
	Pleopod buds on somites 2–6	Pleopod buds on somites 2–6 [see text]*	Pleopodal exopods with 11, 11, 11, 9, 5, setae	Pleopodal exopods with 9–10, 11, 10–11, 9, 5–6 setae
TELSON	As in stage I	As in stage I	2 strong dorsal setae	2 strong dorsal setae

Note: Data for *M. pleuracanthus* from Yang, 1967; *M. spinosissimus* from Provenzano and Brownell, 1977.
* [] indicate situation as illustrated, differing slightly from that noted in associated text.

phores. Telson anteriorly with a single golden-orange chromatophore medially. Peripheral ommatidia of eyes reflect blue light, corneas dark with pink highlights.

Discussion

Only limited comparison can be made among the presently known larvae of three species of *Mithrax*. Our data indicate that the zoeae of *M.* (*Mithraculus*) *forceps* are much closer morphologically to at least the first zoeal stage of *M.* (*Mithrax*) *pleuracanthus* (based on features described by Yang, 1967), than they are to larvae of *M.* (*Mithrax*) *spinosissimus* (Provenzano and Brownell, 1977). The similarities are summarized in Table 2 where it can be seen that the only salient differences in morphological features between the first zoeal stages of *M. forceps* and *M. pleuracanthus* are in number of antennular aesthetascs (4 and 3, respectively [but only 2 illustrated by Yang]), the setal formula of the endopodite of maxilliped 2 (0, 1, 5 and 0, 1, 4, respectively), and in the admittedly subjective observation on the presence (*M. forceps*) or absence (*M. pleuracanthus*) of pleopodal primordia. Other carapacial features such as the reach of the rostral spine of the antennule, and the robustness and curvature of the dorsal spine, are not now useful in distinguishing *Mithrax* larvae because of their subjectivity.

The larvae of *M. forceps* and the first zoeal stage of *M. pleuracanthus* both differ greatly from the zoeal stages of *M. spinosissimus*. The zoeae of the latter species are very unusual in that several appendages, such as the maxillulary and maxillary endites, and the endopodites of both maxillipeds, exhibit a reduction in setation as compared to no such reduction in the former species. Such reduction in setal number, in conjunction with a lack of segmentation in some appendages (most notably in the endopodites of maxilliped 2) may be features indicative of an advanced stage in the larvae of *M. spinosissimus,* if decreasing morphological complexity is suggestive of apomorphy as espoused by Lebour (1928). Whether such apomorphy (if real) is characteristic of any other species in the subgenus *Mithrax* (sensu lato) remains to be determined. These reduced numbers are evident from the data in Table 2.

The general form of the telson in the larvae of *M. forceps* and *M. pleuracanthus* is relatively similar to that seen among the zoeae of other Mithracine species. However, the larval telson of *M. spinosissimus* differs from *M. pleuracanthus* (in the same subgenus), and exhibits a form not close to the genus *Mithrax,* but rather to that seen in the Inachine genus *Stenorhynchus* (see Yang, 1976). The differences in telsonal morphology are especially notable in the median notch on the posterior margin, which, in *M. spinosissimus* (and in *Stenorhynchus* larvae) is very well developed, but is very much reduced in *M. pleuracanthus,* and almost totally absent in *M.*

forceps. Indeed, the only telsonal feature shared with any degree of similarity between *M. spinosissimus* and the other two *Mithrax* is the setal formula on the posterior margin, which remains 3 + 3 in all larval stages.

In comparing the zoeal features of *M. forceps* and *M. spinosissimus* we noted in Provenzano and Brownell's illustrations (1977; Figs. 2B, 3A, B) the presence of 5 pairs of pleopod buds in stage I, and the apparent lack of a sixth abdominal somite in stage II. The last feature was especially intriguing because, as far as is known, only larvae of *Micippa* in the Mithracinae exhibit 5 abdominal somites in both zoeal stages. With the exception of *Menaethius* (Acanthonychinae), and *Achaeus, Inachus* and *Macropodia* (Inachinae) all other presently known majid larvae have 6 somites in stage II. However, Provenzano (personal communication) clarified this apparent anomaly, stating that the fifth pair of pleopods in stage I (his Fig. 2B) are probably non-erupted pleopodal buds which may have been visible through the zoeal abdomen. A re-examination of stage II using more powerful optics by Provenzano showed that a sixth somite was definitely present but the dividing suture between the telson and that somite was very fine, and the associated pleopod buds were extremely small and easily overlooked. Thus, *M. spinosissimus* exhibits 5 abdominal somites in stage I, and 6 in stage II, as seen in other Mithracinae larvae. Provenzano also informed us that a mandibular palp was present in stage II, thereby providing yet another feature of agreement between the zoeae of *M. spinosissimus* and *M. forceps*, and consequently with other known Mithracine larvae.

In regard to other larval features within the subfamily Mithracinae, or even more broadly considered, among the family Majidae, little can be said. We tend to agree with Provenzano and Brownell (1977) who stated that there are few characters which can be used to distinguish among the larvae of the various genera. We did note, as did Yang (1967) and Kurata (1969) that many of the genera exhibit a remarkable consistency in larval features, with exactly similar formulae in antennular aesthetascs, processes on maxillulary and maxillary endites, in basipodal, endopodal and exopodal setation, and spination on abdominal somites. The chief differences among the larvae of the Western Atlantic genera appear to be in the setal formula on the posterolateral carapace margin, the scaphognathite, and in the general form of the telson. The difficulty in separating majid larvae is therefore probably more often exacerbated by consistency in zoeal features than not. It is obvious that many more studies within the genera are needed before the relative importance of most larval features can be finally determined.

Data on Mithracine postlarval stages are even more sparse, so we must confine our remarks to a comparison between *M. forceps* and *M. spinosissimus* (Table 2). As might, perhaps, be expected in a taxon wherein the adult exhibit so much heterogeneity in form, the megalopae of the two

species can be easily distinguished by their respective overall morphology, although neither resembles in form a minature adult as is true for some anomuran and brachyuran postlarvae. The postlarval stages of *M. spinosissimus,* like the zoeal stages, continued to show reduced or absent setation or segmentation on the mouthparts, in comparison to that seen in *M. forceps*. However, the latter species, like *M. spinosissimus,* now also lacks setae on some appendages, notably the endopodites of the maxillule, maxilla, and maxilliped 1. But the two species may otherwise be easily differentiated using antennular aesthetascs (more in *M. forceps*), scaphognathite marginal setae (less in *M. forceps*), second maxilliped endopodal segmentation (4 in *M. forceps,* 5 in *M. spinosissimus*), and general armature on maxilliped 3 (exopodite setose, endopodite ischium unarmed, a ring of setae on the basipodite in *M. forceps*; exopodite naked, endopodite ischium dentate, no basipodal setal ring in *M. spinosissimus*). The reduced setation and segmentation in the megalopal appendages of *M. spinosissimus* reflect a situation noted earlier in the zoeal stages, again suggesting that if apomorphy has occurred the postlarval stage of this species may be more advanced than that of *M. forceps*. Larval and postlarval studies on *M. pleuracanthus* and related species should therefore prove most interesting in this respect.

The very close similarity between the zoeae of *M. forceps* and *M. pleuracanthus* raises some question as to the utility of their respective subgeneric groupings in view of the different larval features now known to occur. It is additionally apparent that the larvae of *M. spinosissimus* can be particularly distinguished on morphological grounds from at least one species (i.e. *M. pleuracanthus*) presently occupying the same subgenus. Moreover, the data presented above show that *M. spinosissimus* is clearly less related in several zoeal and megalopal features to other members of the subfamily Mithracinae.

Rathbun (1925) characterized the two subgenera primarily by the presence (*Mithraculus*) or absence (*Mithrax*) of branchial sulci in the adults, in conjunction with more subjective features such as the shape and length of rostral horns, and the development of minor teeth of the orbit. However, the very close morphological similarity seen in at least the first zoeal stages of two species which are separated subgenerically as adults primarily by the presence (*M. forceps*) or absence (*M. pleuracanthus*) of branchial sulci, and the inclusion in the subgenus *Mithrax* of the third species (*M. spinosissimus*) which differs not only from the former two species, but in many features from other Mithracine larvae as well, argues for a reassessment of the genus *Mithrax,* and certainly a redefinition of the particular subgeneric diagnoses to take into account recently delineated larval characters. For example, the genus could eventually be separated into two genera (perhaps by elevation of a subgenus after appropriate redefinition), or a third subgenus erected to

accommodate those adults which exhibit larval features obviously disparate from other species.

Acknowledgments

We thank Messrs. John K. Reed and Frank G. Stanton, Harbor Branch Foundation, Inc., Link Port, Ft. Pierce, Florida, for collecting the ovigerous female specimens used in this study. We are extremely grateful to Dr. Anthony J. Provenzano, Jr., Institute of Oceanography, Old Dominion University, Norfolk, Virginia, for graciously re-examining some of the specimens he used in his study, and for providing additional data on larval morphology at our request.

Literature Cited

Gore, R. H. 1971. *Pachycheles monilifer* (Dana, 1852): The development in the laboratory of larvae from an Atlantic specimen with a discussion of some larval characters in the genus (Crustacea: Decapoda; Anomura).—Biol. Bull., Woods Hole 144:132–150, figs. 1–6.

Kurata, H. 1969. Larvae of Decapoda Brachyura of Arasaki, Sagami Bay—IV. Majidae.—Bull. Tokai Reg. Fish. Res. Lab., No. 57:81–127, figs. 1–27.

Lebour, M. V. 1928. The larval stages of the Plymouth Brachyura.—Proc. Zool. Soc. Lond. 1928 (2):473–560, pls. 1–16, text-figs. 1–5.

———. 1944. Larval crabs from Bermuda.—Zoologica, N.Y. 29:113–128, figs. 1–19.

Provenzano, A. J., Jr., and W. N. Brownell. 1977. Larval and early post-larval stages of the West Indian spider crab, *Mithrax spinosissimus* (Lamarck) (Decapoda: Majidae).—Proc. Biol. Soc. Wash. 90:735–752, figs. 1–7.

Rathbun, M. J. 1925. The spider crabs of America.—Bull. U.S. Nat. Mus. 129:i–xx, 1–613, pls. 1–283, text-figs. 1–153.

Williams, A. B. 1965. Marine Decapod Crustaceans of the Carolinas.—Fishery Bull. U.S. Fish Wildl. Serv. 65:i–ix, 1–298, text-figs. 1–252.

Yang, W. T. 1967. A study of zoeal, megalopal and early crab stages of some oxyrhynchous crabs (Crustacea: Decapoda).—Ph.D. dissertation, University of Miami, Coral Gables, Florida, pp. i–xiii, 1–459, figs. 1–94.

———. 1976. Studies on the western Atlantic arrow crab genus *Stenorhynchus* (Decapoda Brachyura, Majidae) I. Larval characters of two species and comparison with other larvae of Inachinae.—Crustaceana 31:157–177, figs. 1–13.

Smithsonian Institution, Fort Pierce Bureau, Ft. Pierce, Florida 33450.